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OBSERVATIONS ON THE AGONISTIC AND BREEDING BEHAVIOR OF *LEPTODACTYLUS PENTADACTYLUS* AND OTHER AMPHIBIAN SPECIES IN VENEZUELA

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ABSTRACT. Observations were made of breeding aggregations of *Leptodactylus pentadactylus*, *Phyllomedusa trinitatis*, *Engystomops pustulosus*, *Phrynohyas venulosa* and *Hyla minuta* in northeast Venezuela. *L. pentadactylus* makes hollows near the water's edge and produces a foam nest where the eggs are deposited. During amplexus and oviposition, the male moves the feet in alternate, coordinated movements over the cloacal openings of the embracing pair, apparently assuring, in this way, proper fertilization and distribution of the eggs, besides beating the foam into the proper consistency. During amplexus, the male shows definite agonistic behavior towards other members of his species or to any other object that may touch him. Quite often fights between males occur. These may last several minutes and consist of standing up and hugging the opponent with the thumb tubercles, pushing, toppling, and apparently embracing, and pulling the adversary towards the breast tubercles.

Engystomops seems to prefer road puddles and fouled water for breeding. Its voice is similar to that of a puppy, and a group of this species will stop calling simultaneously, and for relatively long intervals, when approached by an observer.

Phyllomedusa was extremely abundant in *Dieffenbachia* and other broad-leaved plants. Egg clusters were found on leaf surfaces only. It appears that when leaves of the right size are not found, *Phyllomedusa* does not need to make the leaf nests (funnels) described for many of the species. Besides its normal mating call, the male has a particular release call. It is possible that spent females produce a similar sound.

Phrynohyas venulosa were occupying approximately equidistant positions in a shallow pool. Both this species and *Hyla minuta*, which were extremely common during the first night of observation, had completely disappeared the following night.

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INTRODUCTION

On June 25, 1968, the authors made a trip to the region of Güiria, Estado Sucre, in the Península de Paria of Venezuela, and collected extensively in the vicinity of the village of Rio Salado and on Pica del Mango at a slightly higher elevation (100 m). The conditions near Güiria are xerophytic to mesophytic, but higher up on Pica del Mango the vegetation is quite luxuriant and there is a great abundance of heliconias, Araceae and Marantaceae. Most of the observations reported here were made at Pica del Mango.

The excursion to Pica del Mango was made at night after a heavy rain during the afternoon. As a result of the rain, a depression in the forest had been filled with water to a depth of a few inches. The pool, of about ten by three meters, was undoubtedly temporary, but it may have been in existence prior to the rainy period of that afternoon. The margins, three to five meters beyond the edge of the water, were more or less clear of any vegetation except at one end, where there were a number of broad-leaved Marantaceae and *Dieffenbachia* growing in a thicket. The forest, with its heavy undergrowth of heliconias, *Costus* and Araceae, commenced at about five meters from the edge of the pool. The pool was, however, shaded by two or three large trees that grew near its margins.

The roar produced by frogs calling from the pool could be heard at a distance of about 200 meters. Upon approaching, the noise increased in intensity and became almost deafening. Calling from the leaves of plants were *Hyla minuta*, sometimes three, four, or five to each leaf of *Dieffenbachia*. It was often possible to get three specimens with one sweeping movement of the hand over the leaf surface.

When flashlights were pointed at the water, *Phrynohyas venulosa* were seen to be occupying the pool, spaced in a pattern at a distance of about three to four feet from one another. As there was no vegetation inside the pool, this "formation" could be easily observed.

Also contributing to the uproar coming from the pool were *Leptodactylus pentadactylus* and *Phyllomedusa trinitatis* in great abundance, *Engystomops pustulosus* in lesser abundance, and a few specimens of *Leptodactylus p. petersii*.

LEPTODACTYLUS PENTADACTYLUS

Most attention was given to *L. pentadactylus*, since it was hoped that the following night could be dedicated to the other species

breeding in the pool. Large specimens of *L. pentadactylus* were everywhere; occasionally one would even step on them. In one place, eight breeding pairs were counted in a space about three meters by one meter, a condition reminiscent of the breeding rookeries of some shore birds. Nests were sometimes eight to ten inches apart, but more commonly they were about one foot from one another. As the eyes of *L. pentadactylus* shine red at night, it was not difficult to survey the area and locate and count specimens. Remaining stationary and moving the flashlight around the pool, we counted 60 individuals, but, if it is considered that nests were more abundant in the *Dieffenbachia* thicket, that females in nests were probably not seen, and that many specimens were protected from view by other obstructions, the total number may easily have been double that. More specimens, especially females, were pouring in from the forest all the time.

Most specimens were males, however. Apart from the mated specimens, which were usually quiet in their nests, unattached individuals were moving all the time, the jumps being short and frequently changing in direction. When the butt end of a flashlight was presented to a free male, the animal would move away, and no attempt was made at amplexus (in contrast to what a *Bufo* would

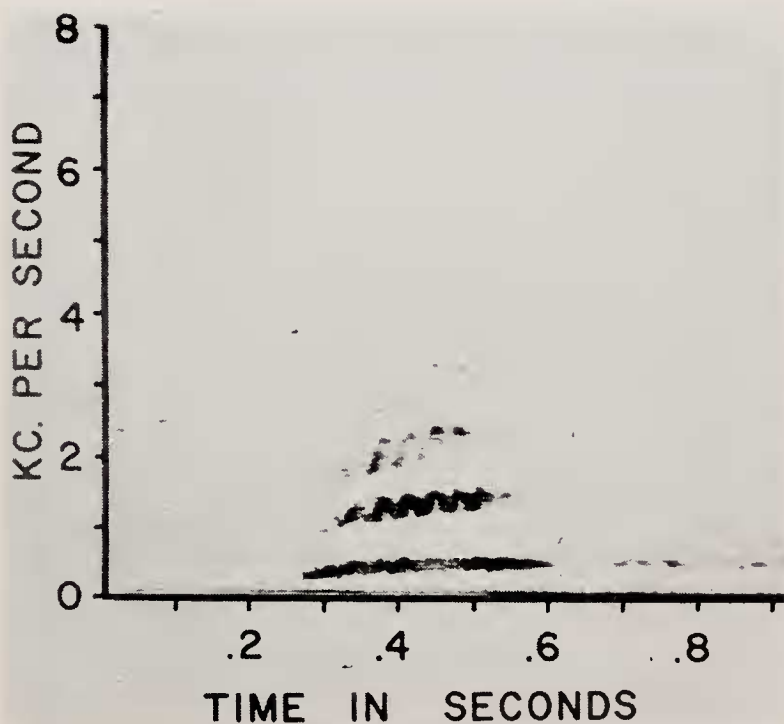


Fig. 1. — Audiospectrogram of the breeding call of *Leptodactylus pentadactylus*, Pica del Mango, Estado Sucre, Venezuela, 25 June 1968.

do). Males were often seen fighting, the two animals rising on their rear legs and attempting to puncture the adversary with their thumb spines by inward embracing movements of their powerful forelimbs. The movements were brisk, and the fight did not usually last more than a few seconds, one of the frogs moving away, or being pushed away, after the first "round." On other occasions, the fight lasted for five or ten minutes, and there was much pushing, toppling (from the raised position), and embracing before the fight was over.¹ These fights created considerable turmoil, and the noise could be heard at a distance of 15 or 20 feet without difficulty. In the plant thicket there was much movement of the plants as the wrestling animals pushed against them.

The male attached to a female showed agonistic behavior towards anything of the right size. If a frog of a smaller species was brought close to the male by the observer, the male would not usually release its hold but would try to push the animal away with one or both arms. If the "attack" were more persistent, or if a bigger animal were involved, it would release its hold and fight the intruder in the usual manner, trying to puncture it with the strong inward movements of the forearms. If the intruder went away, or if it was moved away, the male — if it had been displaced — would give a few short hops near or around the nest, call, and then come back, either to the original female or to any other neighboring female that was nesting and was not pre-empted by another male. If the male had not been displaced, he would just sit above the female, turn around and call repeatedly.

It appears that a male does not have any strong attachment to any particular female, and, if it happens to step on something having the proper consistency, it gives a few short hops, turns around several times, and then attempts amplexus. During this time the female is completely passive.

During the period of observation, it was the authors' impression that the female does not respond, locally, to an individual male's call. Females were coming to the pool, apparently attracted by the males' calls, but once there they did not seem to go to calling males and, when they were moving freely, the males did not pay any attention to them. In practically all cases of matings observed, the females were flat on a depression apparently made by them, and

¹ Similar fights have been described for dendrobatids (Test, 1954; Sexton 1960; Duellman, 1966), *Rana* (Brode, 1959) and *Hyla* (Lutz, Bertha, 1960), but only the latter and *Leptodactylus* are reported to use their thumb spines as offensive weapons.

the meeting — or rather the stepping of the male over the female — was apparently fortuitous, a situation that may explain the continuous and erratic movements of unattached males. To be sure, males were sometimes seen calling from shallow depressions, but they were never seen making the holes, and no females were seen to be attracted to them. Mated males continue to call regularly during the sexual embrace, an indication that the call may constitute an innate mechanism to call females to the breeding site but may not have any local value. It might have a territorial function, but embracing males are often attacked, and not much respect is apparently given to their call. However, after a male has rejected an intruder, he hops around the nest and calls repeatedly, as if he were looking for another “fight,” or as a rooster would, signalling its victory.

As nests (depressions) were sometimes very close together, it was often possible to have several breeding pairs under observation at the same time. In one particular place, there were three breeding pairs about six to eight inches from one another, three unattached males one to two feet away and at approximately that same distance from one another, and two females that arrived from the forest during the period of observation. No foam had been produced in any of the nests as yet. The embracing males were closely attached to the females, with the last finger over the shoulder and the others, including the tubercular thumb, in the axilla. Occasionally there was some shifting movement on the part of the males, perhaps to secure a better position, although it resembled the fondling movements of mammals. One of the males suddenly released its hold and moved away. The female stayed flat (actually slightly concave, the head and posterior ends being higher than the center of the body) in place. After a while, another male came by, apparently by accident, stepped on her, and embraced her. She pushed the mud forward with her forearms, much as a crab would do with its pincers. The occasional “fondling” movements continued.

Another male coming from somewhere else jumped over one of the embracing males, dislodging it. When the attack is sudden in this fashion, the animal is apparently caught by surprise and, if physically displaced, does not usually come back or offer a fight. The intruding male did not, however, take “possession” of the vacant female and, after a while, left the place. In a second case, the attacking male took possession of the female and, in a third, the attacking animal took possession, not of the vacated female, but of another vacant one a few inches away.

The two incoming females wandered into the place at different times. They passed unattached calling males without incident. When a female was captured and offered to a male by an observer, no attempt at amplexus or fight was made. Captured males did not produce a release call or vibrations that could be noticed. No attempt at mating was seen with anything not flat on a depression, although one pair was found in amplexus, not in a depression, but about a foot from the edge of the pool. Probably if a male were to attempt amplexus with another male, the attempt would be met not with a release call, but with strong agonistic behavior. In many instances, males were sometimes found fighting away from nests, but it is possible that the fights originated in nests, as in no case were two unattached males seen to start a fight and neither were males seen fighting females.

One of the observed incoming females settled for a while in a foam nest full of eggs. After some shifting movements, she flattened there for a few minutes but then departed for another depression apparently left by another individual, and settled there. After a while, she was embraced.

The other incoming female did a lot of wandering, trying several sites, passing only inches away from calling, unattached males, and then disappearing for a few minutes. This specimen was probably the one seen later in amplexus near the water's edge. It is not known if this female was grabbed by a male while passing, but this was the only instance in which a mated pair was seen out of a nest (depression).

On one occasion a commotion was heard at the plant thicket and a male was seen trying to clasp the horizontal stem of a *Dieffenbachia* plant. The stem came out of the ground vertically, but about 3 inches from the ground it bent and continued horizontally for about a foot before becoming vertical again. The frog was holding the horizontal portion of the stem (which was about 1½ inches in diameter and quite fleshy) and was trying to clamp it with jerky inward movements of his arms. It is not known if the stem was confused with a female or with a male; it is possible that a fight between two males had been going on and, as one retreated, the other continued to fight with the best possible substitute: the fleshy, slightly raised stem of *Dieffenbachia*. During this unilateral fight, the male was seen to raise its hind legs, first one, then the other, as if attempting to scratch the antagonist with its foot.

When a flashlight butt was pushed at an embracing animal, he released his hold, clasped the flashlight with his arm, moved his arms inward several times, making a noise as the thumb tubercles

hit the metal, and apparently pushed the flashlight tube towards the breast tubercles with his clasping arms. Some "scratching" movement of the hind limbs was also noticed, but again it is not known if this was done to produce harm or to be able to have all four legs on top of the flashlight, which was presented in an oblique position.

The nest is a shallow depression apparently made by the female, who flattens out and moves mud forward with her forelimbs. She also makes sidewise movements, as a *Phrynosoma* would do to cover itself with sand, and may also do some pushing with the hind limbs, but this was not observed. The nest depression is round, only slightly bigger than the animal, and, since it is generally made near the edge, but out of the water, it usually has a little water in the bottom. Some foam nests were at the margin of the pool, but inside the water, and one was associated with floating debris. No central depression or opening can be observed in the foam. In fresh nests some radiating and spirally arranged lines can be seen coming from the center, but these soon dissipate, perhaps because the wandering males do not hesitate to step on nests and other females may flatten up in them as if the foam were non-existent.

In the region of La Escalera, Estado Bolívar, where several foam nests were observed in a shallow pool, these were usually in the water (not deeper than one inch) and associated with sticks, leaves, and other debris. A few were out of the water, but under the leaf litter at the edge of the pool.

Unfortunately, the production of foam could not be observed. In many of the nests, foam was already produced, and in others with amplexing pairs no foam was produced during the period of observation. After the foam is produced, male and female seem to be absorbed in their activity. Every few seconds (about $\frac{1}{2}$ minute) the female dumps her head in the foam and raises the posterior end of the body. The male follows her, and for a while both heads disappear in the foam while both posterior ends are raised above it. Then follows a most interesting movement. The male starts a fanning movement with his feet, moving them up and down, one following the other in a rhythmic, well-coordinated fashion. As the toes are moved over the cloacal opening of the male, they may carry sperm down to the cloacal opening of the female, while at the same time they apparently spread the fertilized eggs out into the foam. Foam, by the way, is flowing between the two cloacal openings during the whole procedure. While this process is occurring, the foam may be seen to increase in quantity. It appears that the fanning movement of the feet may have three functions: passing the sperm over the eggs, distributing the fertilized eggs in the foam.

and agitating the water in an egg beater fashion so that it mixes with the sperm fluid and produces a foam of the right consistency. Substances produced with the sperm or eggs or both may contribute to add viscosity to the liquid.

ENGYSTOMOPS PUSTULOSUS

Some *Engystomops* were observed in the forest pool described above, but apparently this is not their preferred kind of site, as only 10 or 12 individuals were seen here. The same fanning movement observed in *Leptodactylus* was seen in *Engystomops pustulosus*, but in this case mating occurred in shallow water and not in nests or depressions out of the water. *Engystomops* has a notable preference for pools made in dirt roads by passing cars. In these muddy and agitated places they seem to be at their best, calling continuously with a voice that reminds one of a puppy recently separated from its mother. In the Andes (near La Azulita and at Isnotú) *Engystomops* was collected in water discharged from latrines, where it was calling together with *Hyla crepitans* and *L. poecilocheilus* (Isnotú). Approach to a pool in which *Engystomops* is calling must be made quietly as they can stop calling suddenly, as if by signal, and then keep quiet for a while.

PHYLLOMEDUSA TRINITATIS

Another species breeding in the forest pool together with *Leptodactylus pentadactylus* and *Engystomops* was *Phyllomedusa trinitatis*. If the sight of breeding *L. pentadactylus* was grandiose, that of *Phyllomedusa* was spectacular. The Marantaceae-*Dieffenbachia* plant thicket described above was literally loaded with them. Many leaves were bent as a result of the weight, and others had broken at the stem and hung down with several *Phyllomedusa* attached or walking, in monkey fashion, along the stem. Some *Phyllomedusa* were in amplexus, as well described and photographed by Kenny (1966), but females were relatively scarce; quite often a male would grab another male, only to release him upon the production of his release call and vibrations. A specimen that hung from its hind limbs, dead, was "covered" by a male for about one hour. In some places there were bunches of four or five individuals, all apparently attempting amplexus with a female. These bundles hung like grapes; they were never seen on top of a leaf or on the floor, but embracing pairs were sometimes found on broad leaves or on stems.

The movements of *Phyllomedusa* remind one of those of a monkey. The limbs are moved slowly and deliberately, the fingers and toes grabbing the twigs or branches more or less as a monkey would. Obviously, its walking gait is adapted to moving along twigs and small branches, but, when placed on the floor, it can also walk, although it may jump fairly fast too. When *Phyllomedusa* is placed in the sun, the color first becomes spotted dark green on a lighter green background and later, but in a matter of seconds, it becomes dark, bottle green. In the collecting bag in the shade, most were leaf green, but a few were olive brown, and this latter color is kept after preservation. It is stated by Kenny that the non-breeding color is bright green, whereas the breeding color is olive brown. This could not be confirmed, as most of the specimens observed, including amplexing pairs and unspent females, were green. Calling males from San Casimiro, 850 m, were also of a bright green color.



Fig. 2 — Audiospectrogram of the breeding call of *Phyllomedusa trinitatis*, Monte Oscuro, near San Casimiro, Estado Aragua, Venezuela, 15 June 1968.

In one instance a *Phyllomedusa* was seen to be walking along a stem. Suddenly it stopped, more or less "sat," and, while holding the twig with the two feet and one hand, raised the right arm and waved it around as if looking for another twig. On another occasion the animal raised both arms and did a similar operation. It

appears that the animal "feels" the twigs and branches rather than sees them, but this may have been as a result of the light pointing at it. This behavior looked so unfroglike that it was thought to be accidental until it was observed on several other occasions.

Only three or four bunches of eggs (of about 25 or 30), all attached to the upper surfaces of broad-leaved plants, were observed. This is contrary to the situation described in other *Phyllomedusa* (Budgett, 1899; Agar, 1909; von Ihering, 1866) or for this species in Trinidad (Kenny, 1966), where a funnel made from one or more leaves is used as a nest. A. and B. Lutz (1939) wrote that a nest of *P. appendiculata* was found in a hollow of a wet block of stone covered by a fallen tree trunk in a mountain brook. It appears that when small leaves are not available, *Phyllomedusa* can adapt to other conditions.

How *Phyllomedusa* made itself heard under the roaring sound of *P. venulosa* and *L. pentadactylus* is difficult to understand. Perhaps it comes earlier to the pool; or perhaps the scarcity of females can be attributed to this factor. Kenny (1966:16) reports that the females of *Phyllomedusa* are also vocal and that males have a mating call ("huh, huh, huh") and a non-mating call which they produce throughout the night. The authors only heard two calls, one the regular mating call, and the other, a release call (and vibrations) produced by males when other males touch them or attempt amplexus with them. This call is also produced when a male is grabbed by a human or when several specimens are placed together in a bag. It is possible that spent females produce a similar sound, although this was not recorded.

PHRYNOHYAS VENULOSA

Few observations were made on *Phrynohyas venulosa*, in the hope of paying more attention to this species the next day. However, it was observed that they occupy equidistant positions in the pool, that they retain amplexus after capture, that one was seen to grab a *L. pentadactylus* in amplexus and ride it until they both disappeared, and that even when not calling, the two vocal sacs seem to act as floaters, looking as if the animal were wearing water-wing life preservers.

The voice of *Phrynohyas venulosa* has been described by a number of authors. The call can perhaps best be described as like the bleating of a goat, but when many specimens are calling together, the noise produced can be compared to that of a low-flying helicopter or to that produced by automobiles with holes in their mufflers.

The following afternoon, the surface of the pool was seen to be almost completely covered with what, at first sight, appeared to be the pupae of giant mosquitoes; these were the eggs of *P. venulosa*. That same night both *P. venulosa* and *Hyla minuta* had disappeared completely. And they were neither seen nor heard in another pool a few kilometers away, where they were heard abundantly the night before.

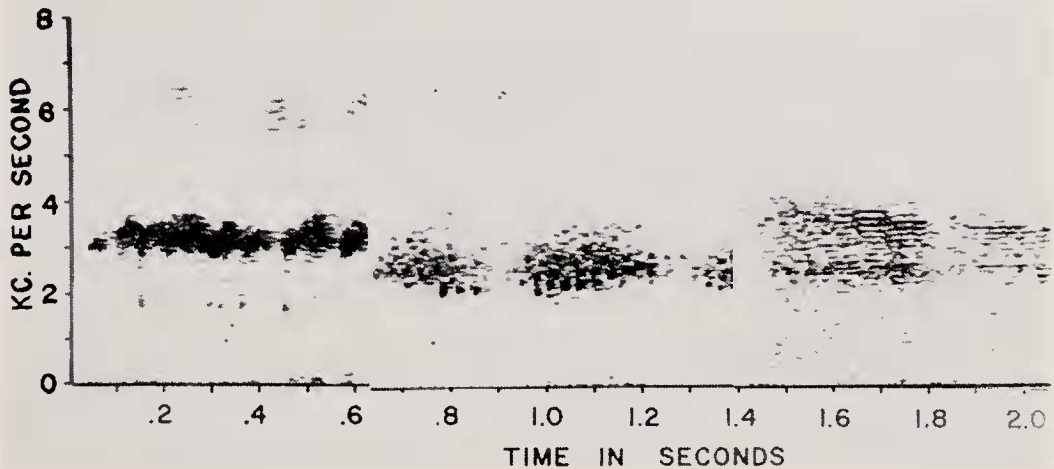


Fig. 3 — Audiospectrograms of breeding choruses. Left, *Leptodactylus podicipinus petersii*, El Pilar, Estado Sucre, Venezuela, 27 June 1968. Center, *Pseudis paradoxus*, Río Salado, Estado Sucre, Venezuela, 25 June 1968. Right, *Phrynohyas venulosa*, Pica del Mango, Estado Sucre, Venezuela, 25 June 1968.

It is not known when the forest pool described above was filled with water. If it was during the afternoon rain preceding our visit, then the breeding of *Phrynohyas venulosa* lasts only one night. During the periods of observation, no ordinary frog predators were seen. *Leptodactylus* can easily swallow *Engystomops*, but it was probably too active, breeding and fighting, to bother about eating. On the first night, two enormous pigs were observed grabbing frogs and apparently eating them (the actual eating was not seen, as the pigs were immediately scared off by the observers, but their insistence on coming back left little doubt about their "intentions"). Three of the *P. venulosa* seen were dead, the other came out of the water dying. The cause of this is not known, but it is not improbable that they accidentally bumped into a male *Leptodactylus*, which can be a dangerous adversary. In one instance, Esteves' hand was accidentally grabbed by a male *Leptodactylus* and, before he could remove it, the animal tried to puncture it with its thumb tubercles

by jerky inward movements and did its best to push the hand against the breast spines. A *P. venulosa* would probably be in serious trouble if similarly treated.

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